Harufumi NISHIDA*: Anatomical studies of a new specimen of *Yezopteris polycycloides* Ogura from the Upper Cretaceous of Hokkaido**

西田治文*: *Yezopteris polycycloides* Ogura の北海道白亜紀産新標本についての解剖学的研究

A piece of petrified fern rachis was handed to me by Dr. Toshimasa Tanai of the Hokkaido University in June, 1980. At first it was discovered by Mr. Mitsutoshi Nihongi and Mr. Takemi Takahashi from Katsurazawa region, Mikasa City, Hokkaido, in 1979 and was delivered to Dr. Tanai by their courtesies. From my anatomical examination it was determined as *Yezopteris polycycloides* Ogura (1930) of which the type specimen was collected by Dr. K. Fujii at Yubari in Yubari City, Hokkaido in 1911.

Yezopteris is a fern rachis whose relationsnip to Cyatheaceae was supposed by similarity of the vascular structure (Ogura, 1930). However, the meristeles in *Yezopteris* were apparently arranged into polycyclic stele that was unknown in any cyatheaceous ferns. Moreover, the type specimen in Ogura's figure did not show any sign of dorsiventrality, so that Andrews (in Boureau, 1970) was led to mention that *Yezopteris* was not a rachis but a stem.

As the present specimen is much larger and better preserved than the type specimen, some unknown anatomical features came out from this study. As the specimen is embedded in calcareous sandy shale, it was treated with 1N HCl solution for the usual peel method.

Yezopteris polycycloides Ogura in J. Fac. Sci. Imp. Univ. Tokyo, Ser. III. Bot. 2(5): 381, Text-figs. 1-4, Pl. XIII. figs. 1-4. 1930; Andrews in Traité de Paléobotanique. IV. fasc. 1: 488, fig. 378. 1970; Ogura, Comp. Anat. Veg. Org. Pteridoph: 405, fig. 459. 1972.

Locality: Ashiyachizawa, Katsurazawa, Mikasa City, Hokkaido.

Horizon: Upper Yezo Group: Senonian, Upper Cretaceous.

Specimen: No. 80001 collected by M. Nihongi and T. Takahashi in 1979

---

* Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University. 1-33 Yayoi cho, Chiba, 260. 千葉大学理学部系統学研究室.

** Contributions from the Laboratory of Phylogenetic Botany, Chiba University, No. 78.

was cut into four pieces. These are deposited in the Laboyatory of Phylogenetic Botany, Chiba Univeysity.

Outlook: The specimen is a rod shape, 17.5 cm in length, one end has the diameter ca. 2.5×3.0 cm tapering to another distal end, ca. 2.0 cm in diameter (Fig. 1). It shows apparent dorsiventrality exhibiting an appearence of a fern rachis. A shallow groove runs along the axis in the center of the possible adaxial surface. Both lateral sides are shallowly grooved that may correspond to the pneumathode. There are no signs of branching through its length and the rachis seems to be a fragment of the petiole. There are large number of ridges on the rachis surface, running parallel to the main axis. Each of them corresponds to the vascular strand which may be surrounded by the sclerenchymatous sheath hardly subject to erosion.

Internal structure: Cross sections are shown in Fig. 1 and 2. The stelar pattern is highly complicated. At the base of the rachis more than 225 meristeles contribute to the seemingly polycyclic stele. However, the stele apparently exhibits dorsiventrality. At the more distal part the number of meristeles

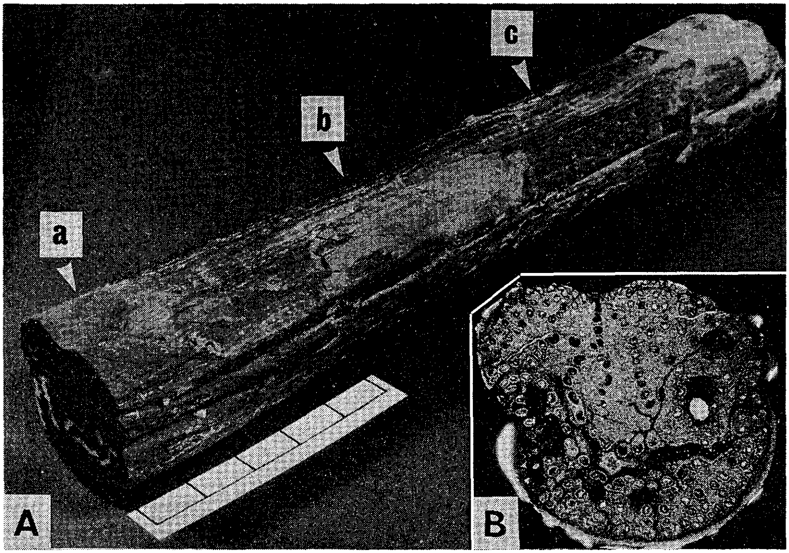


Fig. 1. *Yezopteris polycycloides* Ogura No. 80001. A. General appearence of specimen. Scale indicates 5 cm. Arrows from a to c correspond to cross sections A to C in fig. 2. B. Cross section at the basalmost portion, showing complicated stelar pattern, ×1.3.

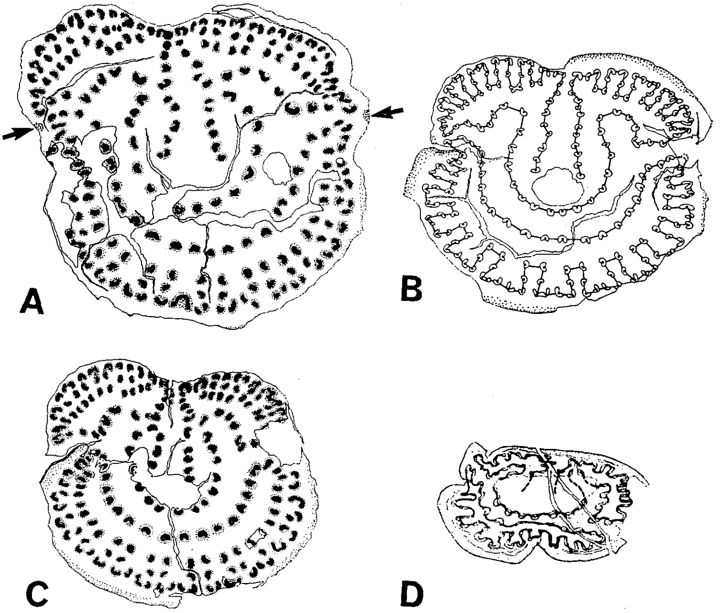


Fig. 2. Successive cross sections of *Yezopteris polycycloides*. A to C, from No. 80001; D, modified from Ogura (1930). A. 1 cm from the base. Arrows indicate the aerophores. B. 7.5 cm from the base. Note the the idealized stelar pattern resembling the Cyatheaceous pattern. Protoxylem of each meristele is shown as a small dot. C. 12.5 cm from the base. Some meristeles are going to fuse into corrugated meristeles. D. Ogura's specimen A in the same magnification as above figures A to C. Note the same stelar pattern as that demonstrated in B. All. Upper side adaxial, ×1.5.

decreases to ca. 190 in contrast to the increasing regularity of the stelar arrangement. The idealized stelar pattern is shown in Fig. 2B. Accord ing to the idea, the stele can be separated into the adaxial and the abaxial groups of meristeles. The adaxial group is *Ω*-shaped opening adaxially, the arms of *Ω* turn deeply into the pith. The abaxial group is banana-shaped with adaxial concave side. It is the typical feature of this specimen that the meristeles are arranged in wavy form, distributing near the periphery of the rachis. The meristele is generally reniform or V-shaped, though some of them connect together on the lateral side or on the convex side to form Wor X-shaped meristele. Such connections of meristeles occur more occasionally as the rachis goes more distal.

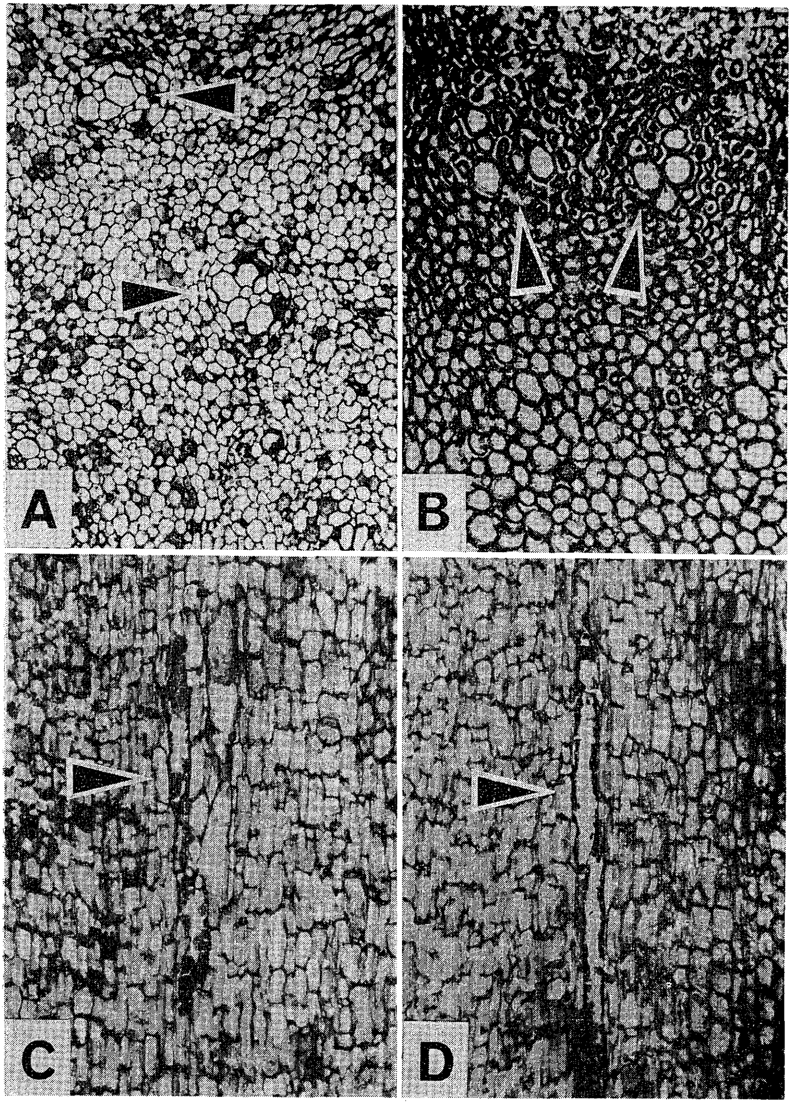


Fig. 3. Fundamental tissue of *Yezopteris polycycloides*. No. 80001. A. Cross section of secretory cells (arrows) in the parenchymatous tissue. B. Cross section of secretory cells (arrows) in the sclerenchymatous tissue of the outer cortex. C. Longitudinal section of a group of secretory cells in the parenchymatous tissue. D. Longitudinal section of secretory cells in the parenchymatous tissue, forming a secretory canal due to longitudinal connection of cells (arrow). A, C and D, ×70. B, ×175.

Histological description: Through the length of the specimen the basal portion is better preserved, exhibiting even the phloem elements as well as other vascular structures. The epidermis is eroded and no dermal appendages are preserved. The cortex is composed of outer well-developed sclerenchymatous layer of more than 20 cells thick and the inner parenchymatous one. The cells of the outer cortex are fibrous to have small diameters than those of the inner cortex, but are much longer. In both cortical layers distribute the secretory cells which are easily distinguishable from the surrounding cells by their large diameters. They distribute solitary or often aggregate to make the mass of several cells (Fig. 3C). The usual parenchymatous cells of the inner cortex are 60 to 80 μm in diameters, 55 to 290 μm in length, while the secretory cells are 90 μm and more than 430 μm, respectively. The diameter of the secretory cells of the outer cortex is rather small, 35 to 70 μm. The pith is composed of cells same as those of the inner cortex. On both lateral sides of the rachis the aerenchyma is present (Fig. 2A, arrows). It is a mass of small, dark-colored, parenchymatous cells loosely agrouped.

The vascular tissue is enclosed by the sclerenchymatous sheath of 3 to 8 cells thick; the diameter of each cell is ca. 30 μm. The vascular bundle is an amphiphloic concentric bundle similar to those of the extant groups of Cya-

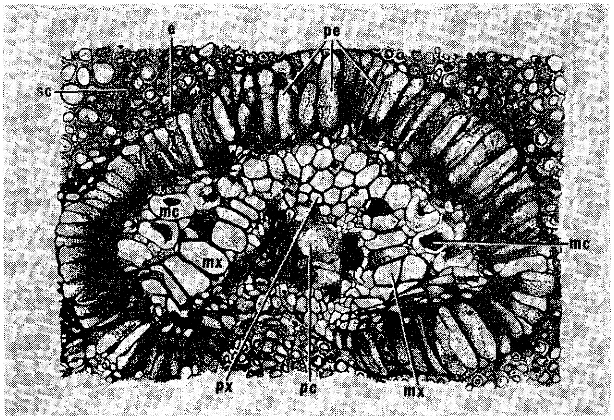


Fig. 4. Vascular bundle of *Yezopteris polycycloides*. No. 80001. Line drawings. Note radially elongated pericycle cells (pe) and large mucilage cell (mc) in metaphloem. e; endodermis. mx; metaxylem. pc; protoxylem cavity. px; protoxylem. sc; sclerenchymatous sheath. ×150.

theaceae in the sense of Holttum (1963). The shape of each meristele is reniform or V-shaped. The epidermis inside the vascular sheath is hardly distinguishable from the percycle caused by poor preservation, but if clearly defined, it is a layer of thin-walled cells. The pericycle exhibits special characteristics in this specimen, that is, there are two kinds of cells different in shape and size; the smaller, orbicular cells (Plate VIII, A) and the larger, radially elongated cells (Fig. 4, Plate VIII, BC). Of what kind of cells is composed the pericycle differs in each meristeles. The diameter of the small cells varies from 18 to 50 μm, and these cells generally line in two rows. The larger, radially elongated cells are thick-walled, ca. 30×130 μm in diameters, rectangular in longitudinal section, 15 to 100 μm (generally 50 μm) in height, and are lined in one row usually (Plate VIII, D).

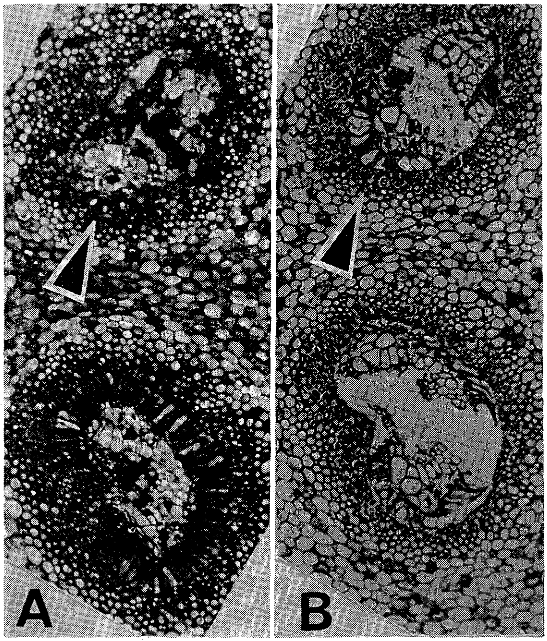


Fig. 5. Cross sections of two neighboring meristeles of *Yezopteris polycycloides* at different level. No. 80001. A. Two meristeles sectioned at a level shown in fig. 1B. B. The same meristeles sectioned at a level shown in fig. 2A (1 cm more distal than A). Compare the shape of pericycle cells in meristeles with arrows. Those in A are round and small, while in B they are large and radially elongated. For more details see Plate I, AB. ×70.

In slide 1 of successive cross sections, which is a section of the basalmost part, there are two types of pericycle in neighboring meristele, one is composed of smaller cells, another is of larger (Fig. 5A). However, in slide 3, 1 cm more distal, the meristele with small-celled pericycle alters to be composed of radially elongated, large cells (Fig. 5B, Plate VIII, AB). So the cells composing the pericycle change their shape in one continuous vascular bundle (meristele), though in a certain cross section their cellular composition is uniform. This is the striking feature of this specimen. The phloem is separated into the proto- and the metaphloem. The metaphloem is composed of small, thin-walled sieve cells and large mucilage cells containing dark-colored materials. The latter is restricted to the convex side of the metaphloem in the reniform meristeles (Fig. 4). In W-shaped meristeles formed by the fusion of the reniform ones the mucilage cells distribute as they do in the latter. The protophloem is present between the pericycle and the metaphloem. It is a lineage of small cells, though is often hardly observable. The xylem is V-shaped in a reniform meristele, and W-shaped in a W-shaped meristele. At the inner concave corner of V- and W-shaped xylem plates locates the protoxylem. The protoxylem tracheid is much slender. The protoxylem cavity is present inside the protoxylem mass (Fig. 4). The metaxylem tracheid is large, oval to rectangular in cross section being connected laterally in one or rarely two rows, the wall thickening is scalariform (Plate VIII, D). The wall thichening of the protoxylem tracheid is not known.

Diagnosis emended: Fern rachis with no superficial appendages. Cross section circular or elliptical, adaxial surface slightly grooved. The stele is similar to that of cyatheaceous tree ferns, being composed of adaxial and abaxial groups of meristeles. The adaxial group is Ω-shaped opening adaxially, with arms curved deeply into the pith. The abaxial group is banana-shaped, convex abaxially. Meristeles distributed near the periphery are arranged in wavy form. In general meristeles V-shaped at the basal portion of rachis, fusing laterally to form corrugated meristeles at more distal portion. Well-developed sclerenchymatous tissue is present in the outer cortex and around each meristele. Large secretory cells are distributed in the fundamental tissue solely, or forming longitudinal canals, or in groups of several cells. Large mucilage cells are present in the metaphloem which developes at the concave side of the meristele. The pericycle of each meristele is composed either of radially elongated, thick-walled cells arranged in one or rarely two rows, or of small, orbicular, thin-walled cells arranged in two rows or rarely one. The radially elongated pericycle cell is rectangular in longitudinal section with low tangential walls.

Discussion Comparison with the type specimen: The arrangement of meristeles of *Yezopteris polycycloides* clarified in this study (Fig. 2B) is similar to that of Cyatheaceae. The stele is composed of two groups of meristeles, adaxial and abaxial. In each group the meristeles distributed near the periphery seem to be arranged in a polycyclic pattern, but actually they are arranged in a wavy row similar to those of Cyatheaceae. The meristeles of the type specimen are arranged in the same pattern as those of the present specimen with unquestionable dorsiventrality (Fig. 2D).

Ogura (1930) reported neither radially elongated pericycle cells nor secretory cells in his description, both of which are the features of the present specimen. But Edwards (1933) mentioned, "There is a suggestion of a large-celled pericycle in some of the meristeles of *Yezopteris polycycloides* Ogura from Hokkaido, as seen in cross sections in the Geological Department of British Museum, but the preservation is too poor for one to feel certain." He also reported secretory cells in the cortical parenchyma.

Other morphological similarities between the type and the present specimen are; (1) metaxylem plate generally composed of a single row of tracheids, (2) sclerenchymatous sheath in outer cortex and around meristeles, (3) the presence of protoxylem cavity. Excepting large mucilage cells seen in metaphloem, which was unnoticed by Ogura because of poor preservation of his specimen, it seems reasonable to conclude histologically that both type specimen and present one originated from plants of the same species. Judging from the general occurence of corrugated meristeles and small size in diameter, the type specimen would be a fragment of more distal portion of rachis than the present specimen.

Affinity: There have been two opinions for the affinity of *Yezopteris*, according to whether one attach phylogenetical importance to the vascular structure or to the arrangement of meristeles. The former was presented by Ogura (1930) who related *Yezopteris* with Cyatheaceae. But it is yet unknown in Cyatheaceae the seemingly polycyclic stele so complicated as in *Yezopteris*.

On the other hand, Edwards (1933) in his anatomical study of *Paradoxopteris* *stromeri* (Hirmer) Hirmer (1927) from the Upper Cretaceous of the Sahara Desert pointed out some anatomical characteristics shared by *Yezopteris* and *Paradoxopteris;* (1) seemingly polycyclic stele, (2) secretory cells among cortical parenchymatous cells placed in alternate positions with vascular strands, (3) pericycle composed of radially elongated cells. From these facts Edwards proposed relationship between *Yezopteris* and *Paradoxopteris*, and also suggested that these two genera had closest relation to Marattiales based on anatomical comparison of above features, especially (1) and (2).

Alvin (1971) pointed out anatomical similarities such as the polycyclic stelar pattern and the position of secletory cells in the fundamental tissue between *Paradoxopteris* and the Cretaceous compression genus *Weichselia* in his comprehensive study on *Weichselia reticulata* (Stokes et Webb) Fontaine from Belgian Wealden, and concluded that *Paradoxopteris* was conspecific with *W. reticulata* or at least congeneric with *Weichselia*. Moreover, Alvin (1971) gave evidences that the reproductive organs of *Weichselia reticulata* had characteristics of Matoniaceae. However, the features of vegetative organs of *W. reticulata* except for its palmate plan of frond were different from those of Matoniaceae and Alvin accepted the family Weichseliaceae Zimmermann (1959), which he considered to have been derived from the same ancestral stock with Matoniaceae. As it is highly probable that *Paradoxopteris* belongs to *Weichselia*, *Paradoxopteris* would be allied to Matoniaceae, neither to Marattiales nor to Cyatheaceae.

As for three anatomical similarities of *Yezopteris* and *Paradoxopteris* noted above, they will be discussed below based on the results of this study. The secretory cells are known widely in various groups of ferns, and it became evident from this study that the secretory cells in *Yezopteris* are never arranged regularly in alternate positions with vascular strands as was observed by Edwards (1933) in *Paradoxopteris*, but are scattered at random. The stele in *Yezopteris* is not polycyclic as in *Paradoxopteris*, but of a complicated cyatheaceous type.

Among fossil ferns the radially elongated pericycle cells are known in *Cyathorachis* (Ogura, 1927) and *Fasciostelopteris* (Stopes and Fujii, 1910). Similar structure is observed in *Weichselia reticulata* (Alvin, 1971). *Cyathorachis* belongs to Cyatheaceae and *Fasciostelopteris*, which was described as a stem, is apparently a fragment of midrib of *Cyathorachis* departing a pinna rachis (Stopes and Fujii mentioned a possibility of its being a midrib, though they rejected that idea without reasonable explanation). Thus the radially elongated pericycle cells are known in different families of Mesozoic ferns and can not be considered to be of phylogenetic significance for relating *Yezopteris* to *Paradoxopteris*.

Edwards (1933) cited many examples of large-celled pericycle in the rachis of living ferns of different groups such as *Alsophila campanulata, Cnemidaria spectabilis, Dicksonia antarctica, Gleichenia flabellata, Loxsoma cunninghamii, Microlepia speluncae, Schizaea malaccana* and *Trichomanes radicans*. However, these examples seldom show such conspicuous radial elongation of pericycle cells as seen in Mesozoic ferns. So it is probable that the pericycle composed of radially elongated cells is characteristic to Mesozoic ferns. Edwards (1933) considered such pericycle as a kind of water storage tissue. Apart from whether his proposal is true or not, the physiological role of such pericycle has to be pursued in relation to relatively large size of Mesozoic ferns that have radially elongated pericycle cells.

Now the affinity of *Yezopteris* will be reconsidered. Its anatomical features are: (1) the stelar pattern is similar to that of Cyatheaceae, (2) the secretory cells are dispersed irregularly in the fundamental tissue, (3) the xylem maturation is endarch to form fundamentally V-shaped xylem plate. These features endorse the affinity of *Yezopteris* to Cyatheaceae as already suggested by Ogura (1927). *Yezopteris* is different from *Paradoxopteris* or Weichseliaceae in: (1) fundamentally non-polycyclic stelar pattern and (2) random distribution of secretory cells. It can be distinguished from Marattiales by: (1) the stelar pattern, (2) the structure and development of xylem, and (3) the presence of the endodermis and the sclerenchymatous sheath both lacked in Marattiales. On the contrary *Yezopteris* exhibits some anatomical dissimilarities to Cyatheaceae such as: (1) the stelar pattern is highly complex, (2) the adaxial group of meristeles is never divided into two bilaterally symmetrical halves, which frequently occur in Cyatheaceae.

These anatomical dissimilarities are enough for one to regard *Yezopteris* as a separate family Yezopteridaceae, though more fossil informations on both reproductive and vegetative organs of this plant are needed for establishing a new family. *Yezopteris* would be an extinct genus that have separated earlier than Middle Cretaceous from the same ancestral stock with Cyatheaceae.

I would like to express my hearty thonks to Mr. M. Nihongi and Mr. T. Takahashi who collected the material for their kindness to donate me it through Dr. T. Tanai of the Hokkaido University, to whom I am also indebted. I am grateful to Dr. Y. Fukuda, Chiba University for linguistick checks of the manuscript, and to Dr. M. Nishida, Chiba University, for encouraging me during the course of this study.

References

Alvin, K. L. 1971. *Weichselia reticulata* (Stokes et Webb) Fontaine from the Wealden of Belgium. Mém. Inst. Roy. Sc. Nat. Belg. **166**: 1-33. Andrews, H. N. 1970. In Boureau ed. Traité de Paléobotanique. **IV**. fasc. 1, 519 pp. Paris. Edwards, W. N. 1933. On the Cretaceous fern *Paradoxopteris* and its conexion with *Weichselia*. Ann. Bot. **47**: 317-341. Hirmer, M. 1927. Handbuch der Paläobotanik. 708 pp. Berlin. Holttum, R. E. 1963. Cyatheaceae. Flora Malesiana. 11/1 (2) : 65-176. Ogura, Y. 1927. On the structure and affinities of some fossil tree-ferns from Japan. J. Fac. Sci. Imp. Univ. Tokyo, Bot. 1 : 351-380. —— 1930. On the structure and affinities of some Cretaceous plants from Hokkaido. J. Fac. Sci. Imp. Univ. Tokyo, Bot. **2**: 381-412. Stopes, M. C. and K. Fujii. 1910. Studies on the structure and affinities of Cretaceous plants. Phil. Trans. Roy. Soc. Lond. B. **201** : 1-90. Zimmermann, W. 1959. Die Phylogenie der Pflanzen, 2nd ed. Stuttgart.

Explanation of plate VIII

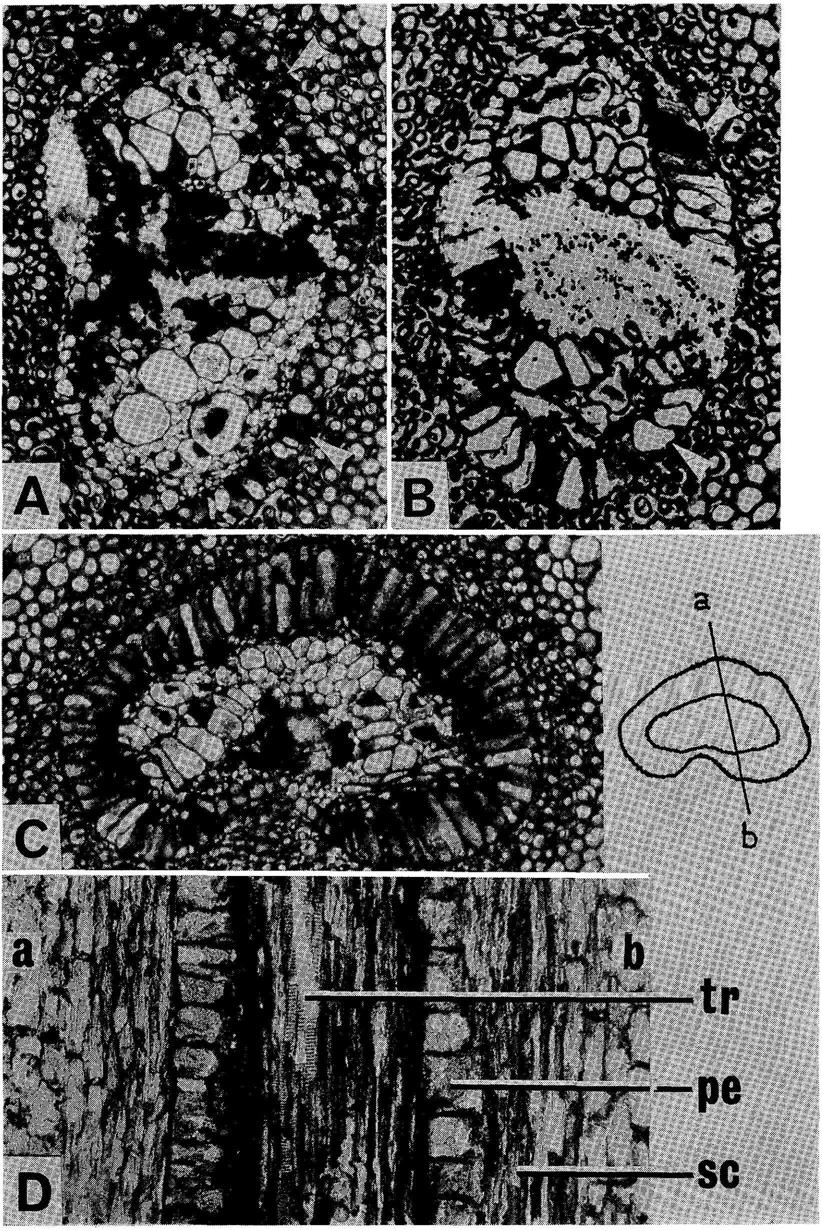
Vascular bundles of *Yezopteris polycycloides*. No. 80001. A and B: Corresponding to arrowed meristeles in fig. 5AB. Note differences of shape and size of pericycle cells (arrows) in a continuous meristele. C: Photograph of the meristele drawn in fig. 3. Line drawing at right hand shows direction of longitudinal section of fig. D. D: Longitudinal section of the meristele shown in C. The letter a, b corresponds to that of line drawing in fig. C. Note rectangular pericycle cells (pe), and scalariform tracheids (tr). sc; sclerenchymatous sheath. All ×150.

* * * *

北海道在住の二本木光利，高橋武美両氏が1979年三笠市桂沢の芦谷地沢で採集されたシダの葉柄と思われる化石の内部構造を検討したところ，かつて夕張市夕張で採集され，

Ogura (1930) が新属新種として記載した *Yezopteris polycycloides* Ogura であることがわかった。新標本は保存が良く，原記載では多環状と言われていた維管束の配列がヘゴ科型であることが明らかになり，さらに，内鞘に放射方向に長い大型の細胞が発達することなど，組織的な特徴もいくつか明らかになった。これらの特徴を化石種を含めた他のシダ類と比較したところ，*Yezopteris* は現在のヘゴ科と共通の祖先から白亜紀中期以前に分化した絶滅群であると推定された。新標本は大型であることから *Y. polycycloides* の葉柄部分と思われる。

□De Vogel, E. F.: **Seedlings of dicotyledons** 465 pp. +2 プレート. 1980. Centre for Agricultural Publishing and Documentation, Wageningen.　最近被子植物の芽生えについていくつかの著書が出版されている。それらの中でマレーシア熱帯に生育する種類の芽生えについての研究を基礎として編められている点が本書の大きな特色である。本書は双子葉類の芽生えについての一般論とマレーシアの双子葉類樹木150種類の芽生えの図説との2部から構成されている。一般論は全体の頁数の約 $^1/_3$ で，芽生えの術語，芽生えの研究史，芽生えの定義，芽生えの形態，機能および変異，芽生えの分類，芽生えの型 Seedling types，芽生えと分類学，芽生えの生態などが扱われている。芽生えの型では芽生えを16型に分類・命名したうえで，マレーシア産樹木でみるとそれらの型が分類体系とどのように関連しているかについて整理し，さらにそれら16型間の類縁関係について考察している。Van Steenis (1972) の Mountain flora of Java の植物画を画いた画家による *Shorea* や *Quercus* などの芽生えが水彩画で20枚ほど挿入されており，目を楽しませてくれる。残りの全部はマレーシア産樹木の芽生えを図説した部分で，全体の約 $^2/_3$ を占める。著者はオランダの Rijksherbarium に所属し，自身で多くの種子をスマトラ，ジャワ，ボルネオなどで採集し，Bogor 植物園内で播いて記載や図を作った。全体によく編められており，多数の文献も引用されているため，分類学的立場からの芽生えに関する文献として推薦できるものである。しかしながら，樹木の芽生えに基づく研究から草本までを含めた芽生え全体に論を拡げている点で論義に飛躍のある部分が散見される。また種類の撰択に分類学的配慮を望みたい点がある。例えばマレーシア固有種を多く取り上げれば，より特色となったであろう。*Desmodium* の芽生えについて Ginkgoana 1 (1973) の私の論文を引用した部分 (p. 119-120) では *Codariocalyx* や *Tadehagi* などについてのデータをも利用すればもう一歩論議が進んだと思う。印刷，製本はよく出来ており，図を多くて読み易い。(大橋広好)



H. Nishida: *Yezopteris polycycloides* Ogura